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In addition microörganisms are internal symbiants in insects and other animals. In the intestine of higher animals, these may elaborate protein from non-proteins, or serve other ends, as preserving a constant digestive flora. In still other locations, as fat bodies, coeca and the like, they may destroy waste products of metabolism, produce digestive enzymes, etc. The exact value of these internal relations, however, is by no means securely established.

## PROBLEMS OF FERTILIZATION

In a book with this title, Lillie has placed in brief and semi-popular form a discussion of the problems of fertilization to which he himself has made notable contributions. Fertilization has long been recognized as a critical and decisive process in all plants and animals in which sex appears, and has appealed keenly to human interest from the earliest times. Every modern step in the study of genetics, variation, inheritance, and breeding from any angle whatsoever has paid tribute to and received support from investigations in the chemical and architectural composition and the behaviour of the egg and sperm as these cells unite in fertilization.

In the first chapter the author traces the history of human speculation and discovery in respect to eggs and sperm and the manner and meaning of their coming together. Few items of biological progress illustrate better the gradual passage from the metaphysical philosophical subtleties of *a priori* reasoning than this field shows. The discovery of the living sperm, by Leeuwenhoek and others, soon after the invention of the microscope, at first only gave a more riotous zest to these speculations. But gradually increased knowledge of the facts, coupled with definite limiting experiments, chastened these theories and led to the recognition of the coördinate value and function of the male and female elements.

The intimate cytological investigations of the last quarter of the nineteenth century finally brought into clear view the full significance of the cell—and nuclear—theory and made possible its final application to fertilization. There has been no more brilliant biological work in any field than that which relates to the behavior of the nuclear elements in maturation and fertilization.

There are two sets of problems at this point "where all the strands of the webs of two lives are gathered in one knot, from which they diverge again and are re-woven in a new individual life history." One group relates to the specific morphological and physiological problems of fertilization. The other includes questions of inheritance. It is to the first of these that the book is directed. Progress in recent years has been in perfecting our knowledge of the actual structures and processes involved in the bringing of these two nuclei together in one cytoplasmic mass; and in the much more difficult and less known realm of the physiology of fertilization, including as it does all the actions and reactions of the external and internal elements of these cells as they unite, as well as the factors external and internal that inhibit or limit these reactions.

Chapter II gives striking expression to the place of fertilization in the life history of organisms. While recognizing the generally accepted view that mature egg and sperm cells are senile cells in the sense of possessing such differentiation that neither alone, under ordinary circumstances, can go on with development, the author feels that the inner meaning of sex and fertilization is not fully expressed by the rejuvenescence and de-differentiation that accompanies union. He recognizes an underlying and "invevitable dimorphism of living matter" which sets them apart from all other specialized and senescent cells. Furthermore fertilization is the vehicle for inheritance both in preserving old qualities and in introducing variations. Thus fertilization furnishes material for natural selection to work on. There is evidence also that the result of the union of contrasting germplasms gives greater vigor in offspring—a further accent upon this underlying dimorphism.

Chapter III deals with the morphology of fertilization. In this chapter the author restates the outstanding steps in maturation, the structure of the elements, the method of bringing the cells into mutual influence, the mechanics of the entrance of the sperm into the egg and the resulting changes in the surface apparatus of the egg itself, the fate of the parts of the spermatozoon and their relation to the ovarian structures.

The author summarizes interestinly the relation of the maturing of the germ cells to the act of fertilization. In the case of the sperm cells the maturation divisions always precede the special differentiation of the locomotor elements. In the case of the ovum, however, there is a great variety in the relation of maturation and fertilization. In echinoderms and some other animals the maturation divisions of the ovum are completed before fertilization. This is the typical condition—of our text books. In many animals, on the contrary, the ovum is unable to complete or sometimes even to begin the divisions leading to maturation until stimulated by the entrance of the spermatozoon. For example, in many vertebrates the first polar body is formed and the nucleus enters upon the prophase of the second but is unable to complete the process without fertilization. In other instances the ovum is able to effect the prophases of the first division, but is checked permanently in the metaphase unless the egg is fertilized. In Nereis and some other Annelids the egg will pass thru none of the maturation steps without precedent fertilization.

These variations impress most strongly the loss of power, almost degenerative in character, seen in the maturation of the germ cells; in contrast with the stimulating character of their union. In these cases where entrance of the sperm is necessary to insure complete maturation, the sperm elements rest quietly in the egg until the maturation steps are finished. The preliminary or external phase of fertilization includes such events as the approach and attack of the sperm cell, penetration of sperm, the response of the cortical egg cytoplasm which aids the sperm nucleus in its progress, the special development of the perivitelline structure, which probably tends to prevent polyspermy and otherwise modifies permeability, respiration, and other metabolic and developmental processes.

The actual or internal fertilization involves the study of the fate of the portions of the sperm cell which enter the egg cytoplasm. These consist universally of sperm nucleus which represents the nuclear chromatin in its most concentrated form; and certain small sperm cytoplasmic elements which differ greatly in different groups of animals—from nothing to a very considerable portion. The author conceives that the course of the male nucleus in the cytoplasm is due neither to initial direction at penetration nor to attractions between the nuclei; but rather that they move together because of independent movements forced upon them by the stresses of a common cytoplasm, somewhat as two chips might come together in an eddy.

A most profoundly important morphological problem is that of the equivalent and representative character of the chromatin (chromosomes) of the male and female nuclei. About this item has arisen our most adequate interpretations of inheritance from the embryological side.

The other constituents of the sperm to enter eggs are the beak and tail of which there is no demonstrable history; the sperm centrosome, and mitochondria. There is great variation in respect to sperm centrosomes. The author believes that the sperm aster which arises shortly after the sperm has penetrated the egg cannot be attributed uniformly, if at all, to a sperm centrosome entering with the sperm. The middle piece of the sperm does not enter at all in Nereis; and by mechanical means he has been able to remove the middle piece from sperm nuclei—which nevertheless formed the aster at the customary place and in the usual way. Aster formation then he ascribes to the influence of the sperm nucleus itself rather than to an inherited centrosome.

While not denying that sperm mitochondria, which have been traced for several cell generations in cleavage, may function in the egg, the author holds that they show no evidence of being dimorphic in composition or behavior when compared with those of the egg itself.

One remaining substance, the egg cytoplasm is still to be mentioned. In quantity it is quite the most impressive material to be considered. It must determine in high degree if not exclusively the early embryonic steps. These processes and characters may fairly be said, therefore, to be exclusively maternal in their origin. And the cytoplasm, from the point of view of inheritance, might well be the determiner and conserver of the basal racial trends. The maternal cytoplasm would, however, be gradually used up—and all restoration and increase would be the joint product of the cytoplasm and the biparental nucleus. Thus we might expect the later stages of individual development to be increasingly the product of this nucleus, unless there may be some permanent elements in the cytoplasm which grow and reproduce independently of the nucleus.

Under the caption "Physiology of the Spermatozoon," Chapter IV discusses such questions as these: What sensitiveness and modes of behavior have spermatozoa? To what extent are their actions determined by the conditions of the media? What are the optimum conditions for them? The principal facts about them may be summarized as follows. Spermatozoa are shown to be exceedingly sensitive to some external conditions. While usually without motion in the testis and the ducts leading from it, they readily become mobile under the operation of various natural and artificial media. They are little influenced by light or gravity. They are sensitive to changes in osmotic pressure, and more so to increase than to decrease of it. Temperature affects the rate of their movement as measured by the time required to aggregate.

The most important factors in determining the behavior of spermatozoa are contacts and the chemical character of the medium. The chief ways in which these factors operate are (a) by increase or decrease of activity, (b) by producing aggregations of spermatozoa thru chemotaxis; (c) by reversible agglutinations; and (d) by thigmotactic adherance to surfaces of various kinds.

Various media, differing in different types of sperm, may activate quiet sperm. In mammals the secretions of the prostate and other glands normally activate sperm. In other instances sperm may be made active by physiological salt solution, by sea water, with or wihout an excess of OH ions. In general the medium in which insemination normally takes place will render them active. For the most part they are extremely sensitive to changes in these media. Addition of acids to sea water decreases activity and causes paralysis. Saturation of sea water with $CO_2$ completely paralyses. Alkalies in general increase activity up to the lethal strength. Other things being equal the degree of activity of spermatozoa is a function of the H ion concentration of the medium.

Fresh active sperm in suspension in their inseminating medium rapidly aggregate in masses. This action is due to rapid $CO_2$ production by the moving spermatozoa themselves. They collect in any region of increased $CO_2$ tension. This proceeds as tho the spermatozoa assume a positive orientation in a $CO_2$ gradient. The author believes this is the actual explanation of the reaction.

Now it is known that the eggs of marine animals normally give off into the sea-water, before fertilization, $CO_2$ and other complex substances. These egg secretions have striking effects upon the sperm. In some types of sperm these secretions make immobile sperm highly motile. They also produce aggregation of the sperm, such as is shown about $CO_2$-producing centers; and, third, in some species cause a coherence or sticking together of the heads of the spermatozoa, —called "agglutination," which is quite distinct from the chemotactic aggregation. This agglutinating reaction is reversible; that is, the masses may later break up without the sperm suffering any toxic or other effect. The specific substance that causes agglutination is a peculiar product of the egg. It is not contained in the blood or other extracts of the female body. It is produced only by mature eggs, and ceases when they are fertilized. Its production is coincident with the period during which the egg may be fertilized.

The agglutinating substance is colorless; will not pass thru a Burkefeld filter; will pass thru specially hardened filter paper; is non-dialyzable; is only slowly destroyed at the boiling point; preserves its power in sea-water for months, tho it does slowly disintegrate. Chemical and efficiency tests suggest that it has analogies to the ferments.

The union of egg and sperm depend upon motion of sperm to the egg, adhesion to it and penetration of it by the sperm. It is clear, therefore, that the egg secretion by stimulating motion in the sperm, by guiding its orientation, by developing an adhesive surface thru the agglutinating substance—all coupled with the well established thigmotropic reaction of the sperm, furnishes a highly adjusted situation leading toward this event.

In Chapter V the general relation of the physiological events involved in fertilization is treated. There are certain essential tho elementary features about the intimate process of fertilization which the author does well to stress. For example, fertilization must not be thought of as synonymous with the penetration of the egg by the sperm. Fertilization is as a matter of fact a complex and progressive reaction, of which penetration is an initial portion. It is a very definite series of events complete only when the inseminated egg is fully capable of development and of transmitting the inherited characteristics. Furthermore, fertilization is an "irreversible" reaction when considered as a series. That is to say, after responding normally in the cycle of reactions neither of these cells can go back to the physiological state that existed before that response. Most cells, after being stimulated and functioning, are able sooner or later to return to the beginning phase and repeat the cycle. The egg and sperm are in a critical phase which prohibits reversibility.

Fertilization is possible only for a very limited and very definite time in the life of the spermatozoon and egg. Unripe sperm will not fertilize and unripe eggs cannot be fertilized. Both become aged and cease to be functional. The time required for this differs. Ordinarily it is very short, especially after sperm or eggs reach an external medium; altho sperm may remain functional in the sperm ducts of the male for weeks or months. Similarly, where internal insemination occurs, sperm may remain potent for considerable periods; as in fowls, for two or three weeks, or in bats for as much as six months.

The author adduces some most interesting experiments to show the rate of decrease in fertilizing power in sperm, and that motility is not the sole measure of fertilizing power. In respect to both sperm and ova the writer believes that the power of fertilization depends upon the presence of a specific substance produced by the cells. In the case of the sperm he regards it as probable that this is identical with the agglutinable substance of the spermatozoa. In the egg the onset and waning of the capacity to be fertilized is due to the formation and loss of a (hypothetical) substance which he calls *fertilizin*. Fertilization itself, in all kinds of eggs, causes loss of power to be fertilized.

Fertilized eggs differ from unfertilized eggs in that the permeability of the membrane is increased, as is shown by increased use of oxygen after fertilization in some eggs, by increased escape of $CO_2$ and other substances, by more rapid transfer of water by osmosis, by taking up of intra-vitam stains, etc. Fertilized egg cytoplasm is less fluid than before fertilization—which is interpreted as a gelation phenomenon. Chemically the fertilized egg loses the power to produce the substance that causes agglutination of the spermatozoa.

The activating effect of the sperm upon the egg consists physiologically of two different and progressive parts; (1) the cortical changes which usually closely follow upon penetration, but which in some types of eggs may be shown not to depend on penetration; and (2) the internal progressive series of processes which seem to be completed about the time of the union of the nuclei. In this internal work does the sperm activate the egg by means of a substance, which itself gradually releases? Or does it progressively activate some substance already in the egg?

In Chapter VII this special problem of activation of the egg is taken up in detail, and may be considered in three phases; the production of the changes at the surface of the egg in the plasma membrane and the cortex; second, the activation of the internal protoplasm; and finally the operations of the combined nuclei, leading up to karyokinesis and cleavage.

The evidence seems conclusive that the egg produces and possesses all the activating substances. The spermatozoon merely releases these or causes their development, and does not furnish the substance itself. This is evidenced by the fact that polyspermy does not in any way accelerate the process. The author's view may be summarized as follows:

First interaction—egg on sperm: The egg secretes in the process of maturing substance whose first manifestation is its agglutinizing or binding effect on the sperm. This, supplemented by the thigmotaxis of the sperm, secures contact—and penetration of the egg by the sperm.

Second interaction—sperm on cortical portion of egg: Upon contact and penetration by the sperm there is a cortical change in the egg, which prevents further reaction of the egg to other spermatozoa. In some eggs this shows as an elevation of a "fertilization membrane." This starts at the point of impact and proceeds at a rapid, but measurable and varied, rate around the egg. Beneath this membrane, however, in the cortex there is a "wave of negativity" that is more rapid than the membrane formation and makes the whole cortex immune to further sperm action sometime before the membrane is elevated. This seems to be the really significant reaction.

The author believes that the essential activating substance which produces this cortical fertilization change in the egg is the same as that which produced the agglutinating of the sperm. He calls this substance "fertilizin." The sperm introduces a substance which releases the activities of the fertilizin. This produces the instantaneous change in the cortex. The identity of the fertilizin with the agglutinating substance is based upon the following considerations. Eggs before beginning the secretion of the agglutinizing substance cannot be fertilized; eggs after fertilization are incapable of reaction to entering sperm, and in such eggs all the agglutinating substance also disappears; eggs artificially activated likewise cease to produce agglutinizing substance; washings which cause a decline in the presence of this substance cause the decline also of power of being fertilized. Thus the sperm agglutination and the fertilization activation are completely parallel and coincident, and hence are either produced by one substance with a dual action or by two substances most remarkably yoked. The former is the simpler hypothesis.

Eggs which have been producing abundant fertilizin, sufficient to charge many hundred times their own bulk of sea-water, immediately cease after fertilization, and the eggs no longer agglutinize spermatozoa nor react to them. The author believes this does not mean that the power of secretion is merely exhausted, but that the entrance of the sperm causes this agglutinating side chain of the fertilizin to combine with some substance, and thus the changed cortex becomes completely incapable of further sperm reaction. This substance he calls anti-fertilizin.

The existence of such substance in the interior of the egg which unites with and neutralizes fertilizin is shown by this experiment. The fertilizin of maturing eggs may be collected in sea-water. Then the eggs themselves may be repeatedly washed until they almost cease to produce fertilizin. If these washed eggs be shaken to pieces in the sea water containing their own fertilizin the latter is neutralized. Normally it would have kept for considerable periods. Fertilizin then is necessary for fertilization. As soon as fertilization is effected it disappears from the cortex and further fertilization is impossible. It has been shown that a concentration of egg fertilizin may produce parthenogenesis in eggs of the same species. On the other hand sperm extracts will not activate eggs.

Third interaction—the cortex and sperm with the interior: The activation of the deeper cytoplasm might be effected by the advancing sperm, or progressively from the changed cortex, or both. Spermatozoa that succeed in penetrating into immature eggs or into eggs already reacting have no effect on the deeper protoplasm. Portions of eggs in a state to be fertilized can themselves be fertilized. The author, quoting from work of Chambers yet unpublished, cites experiments showing that dissections of fertilizable eggs *containing* *the internal protoplasm alone* can not be fertilized. Whereas if this inner protoplasm remains connected with cortical material the mass is fertilizable, and the perfection of the latter events is a function of the amount of cortical material present. This determination seems crucial in respect to the essential soundness of distinguishing the superficial from the deeper phenomena, and of considering the processes in the cortex rather than the spermatozoon itself as the activating agency in the deeper protoplasm.

It is suggested that this fertilization product in the cortex may exert a ferment-like action, or bodies formerly solid may become liquified, and thus penetrate into the depths of the egg. These problems are yet obscure. Evidently the cortical combinations release substances that produce metabolic changes, including increased consumption of oxygen, and the initiation of development.

Fourth interaction—of the nuclei and the cytoplasm: Little can be said at present relative to this. The action that brings the two nuclei together the author holds to be merely the parallel effect of the cytoplasmic stresses working upon both, rather than to any attraction between the nuclei themselves. The supreme problem in this connection is the coördination of the various factors and processes that lead up to nuclear division. It is a matter of timing these two nuclei with quite diverse history—and both of these to the cytoplasm. In this process the leading role is taken by the sperm nucleus. The intricate character of this timing process is realized by recalling the various periods in which the sperm enters in various eggs, in relation to the maturation divisions of the egg itself: it may enter during the resting stage following completed maturation; or in the midst of the maturation mitosis; or before the process is well under way. This tuning or timing process may well be considered a mutual one. It is not unreasonable to suppose, with the author, that the sperm nucleus has been "fertilized," and thus rendered physiologically potent as well as synchronized by its experiences in the cortex and thus made relatively dominant in the later stages of internal reaction. The sperm aster would be an instance of this increased rôle.

Chapter VI deals with problems of *specificity*. This means the investigation of the question as to whether ova and sperm, with this well analyzed group of fertilization interactions we have been studying, are thus attuned to each other by such specifically exact adjustments that they are limited to each other. There are two possible aspects of this: (1) Can sperm penetrate other kinds of cell beside the ovum? or (2) Can sperm and eggs of different species of organisms unite and effect fertilization?

In respect to the first problem some claims have been made of sperm penetrating epithelial cells of the uterus, and even cleavage cells of the developing blastula. These findings are not confirmed and are in great doubt. Numerous negative findings are recorded where the sperm have abundant opportunity to penetrate the epithelia of oviducts. Furthermore, the agglutinating product of eggs is specific. No other body fluid, secretion, nor tissue-extract is capable of agglutinating the sperm. We may say then that eggs and sperm seem to be utterly specific from the point of view of their tissue differentiation.

The specificity of the fertilization can be advantageously studied in those animals in which fertilization is external—as echinoderms, teleosts, and amphibia. The studies involve the crossing of different species, genera, classes, and even phyla. Attempted self-fertilization in those forms which usually cross fertilize is also a fruitful field for experiment. Incompatibility—an inverse measure of specificity—may show itself in very varied degrees. In certain combinations, as some species of frogs, the eggs do not react at all to the foreign sperm. In other animals, foreign sperm may start the cortical changes but be unable to penetrate. This is often the case in crossing different genera, classes, etc. In some cases they may penetrate and fail to activate the deeper protoplasm or unite the nuclei. In some cases where the nuclei unite, the sperm chromatin may be eliminated during cleavage, as between some species of Echinus and in crosses of Arbacia with Echinus. In these cases the resulting embryos have purely maternal characteristics. Even in cases where the male chromosomes are retained the development may be partial or otherwise abnormal. In some instances there is complete and normal development, but the hybrid itself is sterile. The hybrids from certain crosses seem perfectly normal and fertile. This makes a most instructive series showing all degrees of compatibility from perfect to zero. It expresses itself in the possibility or ease of fertilization; in the completeness of the reaction; in the tolerance of the chromosomes;

in the initiation of development; in the stage to which it may go; in the viability, the normality, and the fertility of the offspring.

From a survey of the numerous experiments with eggs and sperms of echinoderms, fishes and amphibians—the author concludes that there are both specific and non-specific factors in fertilization. These may be outlined as follows:—

1. There is some specificity in the agglutinating effect of egg secretions. Some sperm have been shown to be uninfluenced by heterologous egg secretions. More investigation is needed on this point.

2. There is unquestionably specific resistence in the normal cortical reaction of eggs to heterologous sperm. Here is the most common block on fertilization. It very generally exists in crosses outside the species and increases with the remoteness. It is found, however, in self-incompatible hermaphrodites. It may be overcome by staling and by the use of chemicals. While there may be physical elements in this cortical adaptation, whereby homologous sperm is favored and heterologous discouraged, the chief factor is almost surely a chemical one.

3. The next stages of activation seem little or not at all specific. Any spermatozoon, apparently, after having produced the cortical reaction may pass on and call forth the same general internal events as the homologous sperm. If chemical means have been used to secure the entrance of the sperm, these can still pass into the cytoplasm and accomplish union. This has been done by means of Mollusk sperm in Echinoderm eggs.

4. Another block, which is of a specific nature, appears in the later stages of activation after the union of the nuclei. This is shown by the elimination of the male chromatin. Clearly similar incompatibility might exist, quite equal to the prevention of normal development, which might still fall short of this elimination. The author believes that the whole problem of specificity in fertilization is closely related to that of sperm agglutination by the egg secretions, which has been shown to be completely parallel to the cortical reaction of eggs in fertilization.

The reviewer has undertaken thus to give a somewhat extended account of the argument in this very suggestive book because the book itself does so well what the *Transactions* have been trying to do for the members of the Society by the "Summaries of Progress" that have been given from time to time. The necessary brevity of such a exposition is a shortcoming; but possibly even this may guide the reader to the book. The whole discussion illustrates most brilliantly the method of approximation seen in physiological analysis at its best.

**The Problem of Fertilization, by F. R. Lillie. 278 pages, University of Chicago Press, 1919. Price $1.75 net.**

## APPLIED EUGENICS

Popenoe and Johnson have undertaken in this book to magnify the application of the principles of genetics to human society rather than to discuss at length the biological foundations of inheritance.

In the study of human biology we are quite disposed to ignore the fact that we cannot always judge the germ plasm of an individual by his own personal accomplishments. The authors impress well the fundamental fact that we must get a germinal rather than a mere cultural basis for human improvement, if we would encourage the production of superior and discourage that of inferior persons. A eugenically superior person is defined as one "who has, to a greater degree than the average, the germinal basis of the following characteristics:—to live past maturity, to reproduce adequately, to live happily and to make contributions to the productivity, happiness, and progress of society."

The authors leave to others the statement of the problems of genetics underlying eugenics, and concern themselves much more largely in consequence with the applied aspects of the question The chapter headings sufficiently indicate the thoroughness with which the subject is presented: Nature or Nurture? Modification of the Germ Plasm; Differences among Men; Inheritance of Mental Traits; Laws of Heredity; Natural Selection; Origin and Growth of the Eugenic Movement; Desirability of Restrictive Eugenics; The Dysgenic Classes; Methods of Restriction; Improvement of Sexual Selection; Increasing the Marriage Rate of the Superior; The Color Line; Immigration; War; Genealogy and Eugenics; The Eugenic Aspect of such Specific Reforms as Taxation, Rural Movement, Democracy, Socialism, Child Labor, Compulsory Education, Vocational Guidance and Training, Minimum Wage, Mother's Pensions,